

March 1, 1954

Spread of mutational change along chromosome. The a_1^{m-1} ; a_1^{m-2} control systems

I. Review of previous discussion:

1. Presented evidence showing that b.f.b. cycle results in alterations in heterochromatic elements of chromosomes of complement -- centromeres, ends, knobs and nucleolus organizer.

2. Because new mutable genes appeared in progeny of b.f.b cycle plants, the relationship between altered heterochromatin and their appearances suspected.

3. Presented evidence of induction of Dt-type action in endosperms undergoing b.f.b. cycle where a_1 homozygous.

4. Gave reason for expecting dots of A_1 in sectors -- the state of the a_1 recessive: Produces dots of A_1 in presence of Dt.

5. Recent work with a_1 - Dt system. Changes in state of a_1 found: produce early mutations to A_1 and to pales. This done by Nuffer at Missouri.

6. New positions of Dt found:

a). Rhoades: Dt in his strain located at or in knob in short arm of chromosome 9.

b). Nuffer, analysed strains of maize from South America to see if Dt might be present in them. Found Dt unit in two strains: One from Peru and one from Brazil.

Both of these Dt units behave just as Dt discovered by Rhoades. Can not be distinguished from one another on basis of action of a_1

Positions of Dt units in chromosome complement: One analysed; not in chromosome 9 but linkage with Y suggest it is located in chromosome 6.

This expected, if Dt like Ac. Can have it located in various parts of the chromosome complement.

These results bring resemblance of A_1 -Dt system closer to that known concerning the Ds - Ac system. The somatic segregation found in early sectorials need further investigation for similarities.

In the a_1 Dt system of Rhoades, hidden mutations very much suspected on basis of distribution of dots in the kernels -- not random, but in sectors.

II. Today - wish to show other types of systems than those previously discussed.

1. One involves the spread of mutational changes along the chromosome induced by events at Ds.

2. The other two involve the action of controlling systems that differ from those of Ac or Dt.

3. No time to develop the analysis in detail. Must describe the behavior without much documentation this time.

III. The spread of mutational change along the chromosome.

1. How discovered: In analysis of two cases where Ds between I and Sh, but close to Sh. I Ds Sh Bz

2. Initial tests, showed Ds very close to Sh. Needed large numbers to determine the crossing over between Ds and Sh. This obtained for both cases.

3. The types of tests: $\frac{I \text{ DsSh Bz Wx}}{C \text{ ds sh bz wx}} \times C \text{ ds sh bz wx}.$

a). With Ac in heterozygous parent: One test: 5907 kernels. Only one kernel that might be a crossover between Ds and Sh found.

I Ds sh bz wx kernel.

b). 37 exceptional kernels found: These were I Ds sh Bz in phenotype.

Could not be due to double-crossovers; No reciprocals: C Sh bz .

c). When no Ac in heterozygous parent, crossed to C sh bz wx Ac, no exceptional kernels found; no crossovers between Ds and Sh either.

d). Suspected that the exceptional kernels with I Ds sh Bz were produced by change in action of Sh to sh from Ds event.

4. The tests of the homozygotes:

$\frac{I \text{ DsSh Bz}}{I \text{ Ds Sh Bz}} \quad \frac{Ac}{ac} \quad \text{or} \quad \frac{Ac}{Ac} \quad \times \quad C \text{ sh bz wx no Ac}$

The results:

parentage in cross		I Sh	I sh	"C"Sh	"C" sh	totals
Case I	Female	2,365	16	22	3	2406
	Male	11,442	142	16	22	11,622
Case II	Female	9,082	18	55	2	9,157
	Male	5,004	44	4	2	5,044

IV. Tests of the I sh kernels:

37 were I Dssh Bz. 12 were I Ds sh bz

1. The I Ds sh Bz kernels:

a). In 9 of 37 cases, reverse mutations to Sh occurred. No change in Ds location in the reversions. Two of 9 highly mutable:

I Dssh - I DsSh - I Dssh Ds not removed when mutations occur, nor changed in location.

b). One of the mutables: crossing over greatly modified: Increased 50 % over standard in I to Ds region, and 300% over standard in Dssh Bz region. This appears even when mutation to Sh occurs. Tests conducted over three generations -- crossing over remains high.

c). Other cases where reversions occur -- no change in crossing over in marked regions : I to sh, and sh to Bz.

d). Among the non-reversion group: Distinguished from one another on basis of crossing over: Some show normal amount; some show reduction in sh to Bz interval; some show no crossing over in sh to Bz interval and reduced amount in I to sh interval.

e). In all 37 cases of mutation to sh, normal male and female transmission and viable homozygotes.

f). Conclusions: Mutation to sh occurs when Ds to left of Sh but only when Ac present. No change in location of Ds when this occurs; mutants differ from one another on basis of presence or absence of reversions, and on increases or decreases in crossing over in I to sh, and sh to Bz intervals.

g). In one case - Case II - Ac in chromosome 9, to left of I. In majority of the I Dssh kernels, location or state of Ac was altered coincidentally with appearance of mutation.

2. The I Ds sh bz kernels 12 cases

a). Marked differences exhibited among them:

Plant from one kernel -- bz; non-mutable; no pollen and no kernels formed. Completely male and female sterile.

Others differed with regard to presence or absence of reversions; in viabilities when heterozygous and homozygous; in transmissions through male and female gametes.

b). These 11 formed a graded series.

(1). Sh and bz phenotypes: Normal male and female transmissions; Ds present, to ~~left~~ of bz and right of I. Normal homozygotes; reversions to Bz in presence of Ac but rate very low. No reversions to Sh noted. Chromosome: normal. Crossing over I to sh normal; not tested between sh and bz.

(2). Exactly like above, except that no reversions of sh or bz noted.

(3). Reduced transmission of chromosome carrying the Ds sh bz modified segment through male; no reduction through female; homozygote very inviable. Chromosome normal; crossing over I to sh normal

(4). Very much reduced transmissions through male of chromosome carrying I Ds sh bz segment. Normal transmissions through female; no homozygotes; heterozygotes (1 dose of Ds sh bz segment) very abnormal and quite inviable in some kernels. Chromosome normal in morphology; crossing over to either side of modified segment normal; no crossing over within segment noted.

(5) No transmissions through pollen of chromosome carrying segment; reduced transmissions through female; chromosomes normal; very inviable heterozygotes (1 dose); normal crossing over I to sh and beyond bz. No crossing over within segment noted. No reversions.

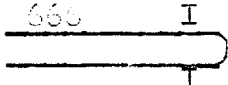
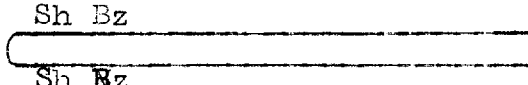
c). In all cases, Ds present. Ds sh bz formed a unit in inheritance, in cases where reduced transmissions occur.

d). The inviabilities of the heterozygotes -- dominance -- not due to a deficiency. Deficiency of whole short arm of one chromosome -- normal kernels.

e). Conclusions: A Ds event, resulted in change in action of Sh and Bz coincidentally. Produced only when Ac present. No change in location that is marked noted. Reversions in only one case -- and this a case of normal transmissions and viabilities of homozygote. Spread of mutational effect probably beyond Bz as indicated by the inviabilities encountered. No change in chromosome morphology noted in any case.

V. The spread of change along chromosome from Ds to I.

1. The "C" kernels in table: These expected on following reasoning:

Females: Ds break:  

One-third of short arm eliminated: This is not sufficient deficiency to eliminate functioning of female gametophyte.

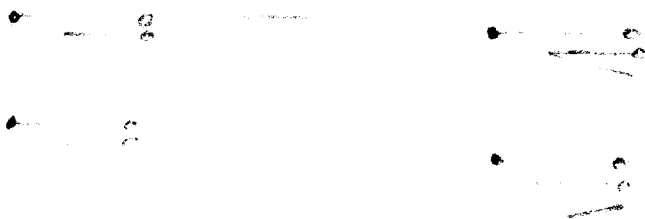
In cross: would expect C Sh Bz kernels from this and they should be variegated for bz due to b.f.b. cycles

2. On the ears, some of the C kernels showed expected bz variegation; others did not show this variegation. Some expected not to show b.f.b cycles: translocations, non-reciprocal could occur occasionally to produce:

..... Sh Bz

3. The analysis of plants from the two types of C kernels:

10 from CBz - C bz variegated class: All as expected:



No Ds present in tests of subsequent generations.

10 from the C Bz, not obviously variegated class:

2 -- non-reciprocal translocations: No Ds.

1 -- former dicentric, centromere removed from one chromatid. No Ds.

4. The remaining 7 in the C Bz, not obviously var. class.

a). All had normal chromosomes 9.

b). All had Ds, just to left of Sh.

c). Divided into two classes on basis of genetic behavior:

4 -- Reduced transmission of the Sh Bz chromosome through male.

3 -- No transmission of Sh Bz chromosome through male.

d); The homozygotes: In 4 cases: colorless kernels. The heterozygotes with C: colored kernels.

"Red I" Ds Sh Bz

<u>Red I</u>	<u>Ds</u>	Sh Bz	Crossing over Red-I to <u>Bh</u> , -- none.
			" " Sh to Bz -- normal.
C	ds	sh bz	

e). The seedlings from the homozygotes: green -- albinescent - dies.
All four cases exactly alike in these respects.

f). The three remaining cases: Like above, except no male transmissions of chromosomes with the "red. I". Form good homozygotes with other $\frac{1}{2}$ cases, however.

g). Conclusions: Action of I, or a deficiency, not seen, to left of Ds. Ds not removed by this. Crossing over in affected segment not seen.

VI. General conclusions:

1. Genes close together in this case. Ds in the middle.

2. Changes occur to both right and left of Ds but Ds not removed or markedly altered in location when change in genic action occurs.

3. These changes are relatively rare -- see table -- but methods used will find them readily. This not easy in cases where Ds not close to several loci -- the majority of cases.

4. Analysis reveals spread of mutational change along chromosome. Not always deficiency, as the case of bz to Bz coincident with sh bz mutation shows.

5. Deficiencies not probably -- should lose Ds in many cases but Ds always present in these cases. Also, a heterozygous deficiency, in cases of Ds sh bz not the explanation.

6. These rare cases can explain the few cases, in study of c-m1, where reversion to C not accompanied by loss of Ds. It remained very close to C. Also, some kernels that reverted to mutable condition noted -- anagin, rare.
(CDs - c to C; This CDs gives c-mutable again.)

The system controlling events at a_1 -m2

A / a Ds and Ac

1. First appearance: in culture having ~~xxxx~~. Change at A_1 ; found in single kernel following cross of female by a_1/a_1

2. Two classes of mutations:

Class I. -- To higher alleles of normal A_1 Kernel dark color; color smooth over aleurone layer. Plant: Dark color; leaves colored in blade.

Class II mutations: Very different: Diffuse -mottled: Quantative expressions from nearly colorless to very dark. Plant: color in sheath, glumes, but none in the blade except in mid-rib and edge of leaf. Sun colored -- requires much sun to form dark color: Upper and lower sides of glumes show this.

Mutations of both classes are stable. No relation between color in kernel in diffuse-mottled class and color produced in plant by same mutation. An almost colorless kernel can produce plant with dark color.

3. Mutations occur in plants -- can recognize both types readily.
Plants derived from variegated kernels -- will show both classes of mutations.

4. The germinal mutations: To full A_1 and to the diffuse mottled class.
All stable in subsequent generations.

5. The frequency of germinal mutations: Examples:

a_1-m2/a_1 m-2 female x a_1^S/a_1^S male

16 ears:	Full A_1	diffuse-mottled	variegated for both types of mutations.
	105	955	2751

Total -- 3811

$1/4$ -- 953.

Each of the diffuse mottled mutations a new one.

5 ears	Full A_1	diffuse-mottled	variegated for both types of mutations.
	31	309	579

total -- 919 $1/3$ -- 306

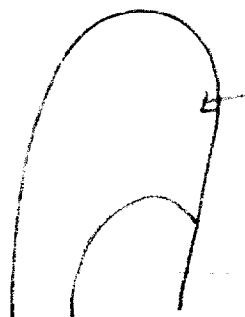
4 ears	Full A_1	diffuse-mottled	variegated for both types of mutants
	47	418	434

total - 899 $\frac{1}{2}$ -- 449.5

Through male -- often same types of ratios observed:

	A_1	diffuse-mottled	variegated	totals	
3:1 ratio	25	180	453	678	$1/4$ 169.5
1 : 1	95	1391	1356	2842	$\frac{1}{2}$ 1421

6. When mutant sector present on ear: $a_1-m2 \times a_1^S$ x a_1/a_1



a_1-m2 kernel = neg. sector. Each diffuse-mottled a diffuse mutation

1:1 for type of diffuse mutation = 1 mutation

7. Conclusion: Some factor present -- segregating at meiosis. When absent from nucleus, a mutation to the diffuse mottled class occurs. These mutants ~~stable~~ from then on.

This factor also segregates somatically -- consequence, a diffuse mottled mutations when factor removed from the nucleus.

Factors probably move about, as does Ac. Reason for the unit ratios observed, when not 1 : 1.

System controlling mutations at a_1 - ml.

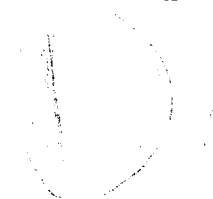
1. Many different types of mutations occur. Many different states arise.
2. All have essentially same system of control of mutations, but most of study conducted with one state -- that producing most of A_1 and some pale mutants -- these last will be shown to be not like mutants previously encountered.

2. The general pattern of behavior of the controlling system.

a). A factor, V^{mod} , for variegation, and modification of action of a_1 locus, present, for variegation to occur.

b). When V present, the kernel color: colorless background; dots of full A_1 and pale areas.

Pr kernels

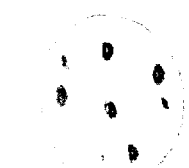


pr kernels



c). When V absent, all kernels are pale, non-variegated.

Pr kernels



pr kernels



d). This phenotype appears generation after generation as stable. Will become mutable when V added: Then, color of background -- colorless, mutation to full A_1 . Again, some of the pale areas.

e). The V shows dosages -- seen in other states very clearly -- controls time of change to full A_1 . Something like Ac in this respect.

d). Linkage of V found -- First linkage - chromosome 6. Table on board.

e). Several sister plants -- V not in chromosome 6.

f). Some plants -- ratios indicate that 2 V factors present, not located in same chromosome.

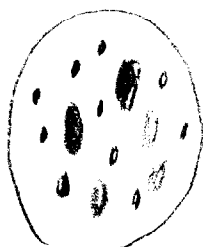
Found in chr. 5. Found another in chr. 7

g). The ratios and behaviors suggest that V is transposing, just as Ac transposes, but these transpositions occur earlier than those of Ac studied.

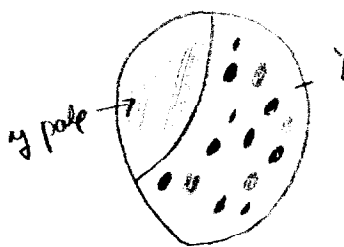
3. The somatic changes to "pale" - give rise to ears: Sectors:

4. The kernels with $a_1\text{-ml}/a_1^s/a_1^s$ $Y\ V/ y\ v / y\ v$:

Normal



Loss of chr.6 in sector



5. Somatic changes in single plant:

1 ear on plant : 1 : 1 for var. to pale

Tiller ear : 3var : 1 pale

Other tiller: all pale.

6. 4 and 6 above suggest somatic segregations of V.

Comparisons between controlling systems of $a_1\text{-ml}$ and $a_1\text{-m2}$

6. Comparisons between $Q, m-1$ and $Q, m-2$, regarding action of factor controlling mutation:

1.) $Q, m-2$ = loss of factor results in change of locus - this is permanent as recombination of factor produces no change.

2.) $Q, m-1$ = loss of factor, ^{you miss} controlling mutation - results in a modified action of the $Q, m-1$ locus: now produce color but this of one type = ~~it varies in~~ ^{no mutation occurs!} ~~pro~~; Factor recombined, action at locus changes; colorless; but now, mutation occurs.

on hand

6229A
comp plants $\frac{Q_{1m} sh_2}{Q_{1s} sh_2}$ $\frac{Y}{Y} \frac{V^{mod}}{N}$

♀♀ +

 $a_1^s sh_2 y n n n$

Plant	Pale		sh ₂ nonpigmented		colorless		Pale		sh ₂ nonpigmented		colorless		Totals
	Y	N	Y	N	Y	N	Y	N	Y	N	Y	N	
6229A ^J	36	58	66	35	0	0	0	0	0	0	85	89	369
" ⑥ ^I	33	54	51	36	0	1	0	0	1	1	101	98	376
" ③	34	52	43	37	0	0	0	1	1	0	85	83	336
" ④	23	65	56	36	0	0	0	0	0	0	90	84	354
" ⑥	34	67	78	37	0	0	0	0	1	0	86	113	416
" ⑦	29	59	58	36	4	1	0	0	0	0	105	100	392
" ⑨ ^I	41	58	50	34	0	1	0	1	0	0	79	115	379
Totals	230	413	402	251	4	3	0	2	3	1	631	682	2622

Totals: 1303 sh₂: 1319 sh₂

1270 Y: 1352 Y

645 pale: 657 nonpigmented: 1320 colorless.

on board

$a, m^2/a, m^2 \times a, s \ a, s$
 $a, m^2/a, s \times a, s/a, s$
 (the a, m^2 carrying families in table)

genes mutations
 segregated

Mr. Jeans.	Fall R.	diff. - within	mutations carrying to fall R. + diff. within	Totals	Ratio of diff. - within.
16	105	<u>955</u>	2751	3811	$1/4 = \frac{953}{3:1}$
5	31	<u>309</u>	579	919	$1/3 = \frac{306}{2:1}$
4	47	<u>418</u>	434	899	$1/2 = \frac{449.5}{1:1}$
3	25	<u>180</u>	453	678	$1/4 = \frac{169.5}{3:1}$
9	95	<u>1391</u>	1356	2842	$1/2 = \frac{1421}{1:1}$
3	18	<u>142</u>	270	430	$1/3 = \frac{143}{2:1}$
2	18	<u>301</u>	157	476	$2/3 = \frac{317.3}{1:2}$